A PETRIFIED FERN SPORANGIUM FROM THE BRITISH CARBONIFEROUS

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ABSTRACT. Small annulate sporangia borne abaxially on pinnules attached to *Psalixochlaena cylindrica* foliar members are described from coal ball specimens collected near Burnley. The *Botryopteris*-like nature of these *Psalixochlaena* sporangia and their small spiny triangular-shaped spores as seen in polar view, indicate that the genus *Psalixochlaena* should now be considered a member of the Botryopteridaceae. *Psalixochlaena* sporangia are quite unlike those of the *Botryopteris* type species, *B. forensis*. Thus plants previously placed in the genus *Botryopteris* which are thought to have *Psalixochlaena*-like sporangia are transferred to *Psalixochlaena*.

THE small Upper Carboniferous fern now known as *Psalixochlaena cylindrica* was first described by Williamson (1878) from coal balls of the Halifax Hard Bed of Yorkshire. The plant has since been noted as a minor constituent of coal ball floras in Lancashire, Holland, and Belgium (Leclercq 1925; Koopmans 1928; Holden 1960). As more was learned about Williamson's plant, its generic assignment has changed several times. Williamson (1878), Hick (1896), and Bancroft (1915), in their descriptions of this plant used the generic name *Rachiopteris*. *Rachiopteris* is not now considered a valid genus, and its various species have all been transferred to other coenopterid fern genera. *Rachiopteris cylindrica* was transferred to *Botryopteris* by Seward (1910) and this generic assignment was followed by a number of subsequent authors (Scott 1920; Leclercq 1925; Bower 1923, 1926; Hirmer 1927; Walton 1940). In 1960 Holden noted the *Anachoropteris*-like abaxial trace curvature of this plant and used this feature as a basis for transferring it from the Botryopteridaceae to the Anachoropteridaceae. At the same time Holden (1960) established the new genus *Psalixochlaena*, with Williamson's plant as the type species *P. cylindrica*. Holden's systematic treatment has been retained by Holmes and Galtier (1975) and Holmes (1977) in recent published descriptions of the *P. cylindrica* branching system.

Sporangia of *P. cylindrica* are not well known. Attached sporangia have not been previously reported, and Bancroft is the only author to describe sporangia 'in association with *R. cylindrica*' (1915, p. 552). Isolated sporangia such as those described by Bancroft (1915) are apparently very common in European coal balls of Westphalian A age, and are known from collection localities where *P. cylindrica* is not reported. Such isolated sporangia have been described and illustrated by a number of researchers (Leclercq 1925; Koopmans 1928; Surange 1952; Pelourde 1910) and have been named *Pteridotheca williamsonii* by Scott (1920). In all cases, these sporangia with trilete spores that are triangular in outline are considered to be referable to *Botryopteris*. Apparently, identical sporangia have been illustrated attached to fronds of the Lower Carboniferous age European species *B. antiqua* (Galtier 1967, 1970) and to laminar foliage of a Lower Middle Pennsylvanian age *Botryopteris* from North America (Good 1979). Plate 72, fig. 5 in this paper shows such a sporangium attached to the abaxial surface of a presumed *Botryopteris* frond from a Lancashire coal ball, and represents the first illustration of this type of sporangium actually attached to a European Westphalian-age *Botryopteris* specimen.

The present paper reports on attached sporangia produced by the plant *Psalixochlaena cylindrica*. Sporangia and spores of *P. cylindrica* appear indistinguishable from those already known attached to Lower Carboniferous and Westphalian age specimens of *Botryopteris*.

[Palaeontology, Vol. 24, Part 3, 1981, pp. 483–492, pls. 72–73.]

MATERIALS AND METHODS

Specimens used in this study were obtained from coal-ball petrifications collected at the tip of the now disused Rowley Colliery near Burnley (O.S. sheet 103, GR 859332, 1:50000 map series). According to local mine officials, coal balls from this tip originated from both the Rowley Colliery and the nearby disused Bank Hall Colliery (O.S. sheet 103, GR 847335), both of which mined the Union seam of the Westphalian A lower productive coal measures. The North American age equivalent of this horizon is Early Pennsylvanian.

Specimens were prepared for anatomical observations using the cellulose acetate peel technique of Joy, Willis and Lacey (1956). Spores from individual sporangia were freed from the calcite rock matrix by maceration with dilute hydrochloric acid. The acid was placed in a wax dyke erected on the coal-ball surface around the sporangium to be macerated. The dyke minimized matrix contamination of the maceration. Slides and peels of the specimens described are deposited with the Paleobotanical Collection, Department of Botany, The Ohio State University, Columbus, Ohio.

DESCRIPTION

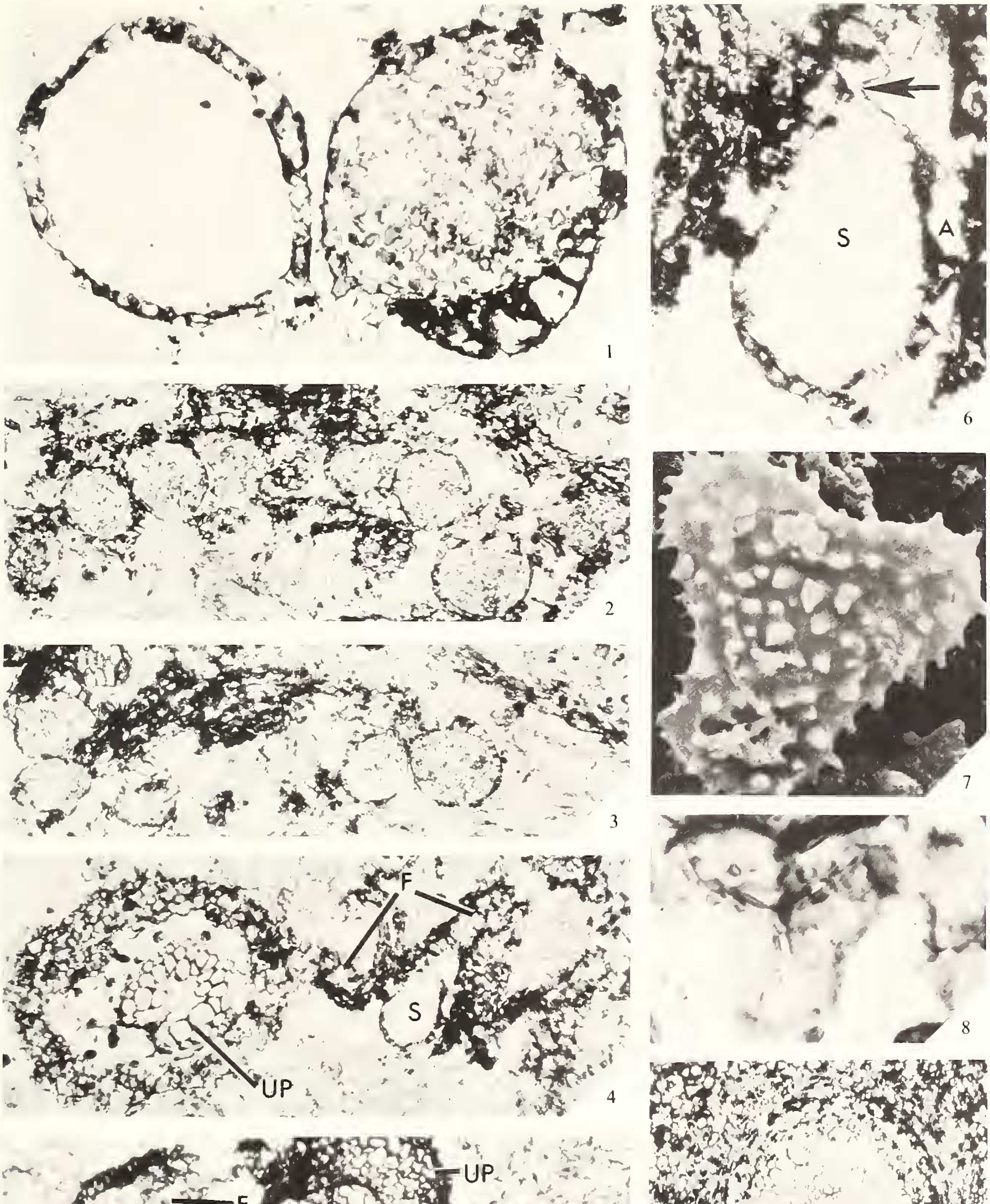
Most of the specimens which form the basis of this study, including all of the illustrations except Plate 72, fig. 5, were obtained from a single coal ball. The coal ball contains numerous *P. cylindrica* stems, characteristically with two or three groups of mesarch protoxylem (Pl. 72, fig. 9), as well as numerous *Psalixochlaena* foliar axes, isolated *Botryopteris*-like small annulate sporangia, poorly preserved laminar fern pinnules, and the usual assortment of lycopod leaves and *Stigmaria* roots. The only plants recognizable in this coal ball are *Psalixochlaena* and lycopods. There is no evidence of *Botryopteris* stems or foliar members. The association of *Botryopteris*-like sporangia with *P. cylindrica* vegetative material in the same coal ball, suggested the possibility that such sporangia were also produced by *Psalixochlaena*.

Individual sporangia are nearly spherical, measuring 280–425 μm in diameter, with an average diameter of 350 μm. The sporangium wall is one cell layer thick and composed of small thin-walled cells except where large thick-walled cells produce a bulge on one side of the sporangium marking the position of the annulus (Pl. 72, fig. 1; Pl. 73, figs. 3, 4). Attempts at macerating entire sporangia out of the rock matrix were unsuccessful, but serial sections suggest that sporangia in the *Psalixochlaena* coal ball are identical morphologically to the *Botryopteris* sporangia shown in line drawing reconstructions by Galtier (1967) and Good (1979).

Sporangia are attached by short stalks either singly (Pl. 72, figs. 4, 6; Pl. 73, figs. 1–4) or in pairs (Pl. 72, figs. 1, 3) to what are believed to be laminar pinnules. Attachment is either abaxial (Pl. 72, fig. 2; Pl. 73, fig. 1) or lateral (Pl. 72, figs. 1, 3). Cell preservation in the tissue to which the sporangia are attached is very poor, and it is therefore not possible to differentiate with certainty between palisade or spongy mesophyll or to find stomata. Nevertheless, the morphology of this tissue resembles that of pinnule cross sections (Pl. 72, figs. 2, 3; Pl. 73, fig. 1 at *f*). Attempts to obtain cross sections of the tissue to which the sporangia are attached were unsuccessful, suggesting that this tissue does not consist of a long narrow axis, but is something broad and flat such as a pinnule. Galtier (1970) shows reconstructions of similar sporangia attached to small axes attributed to *Botryopteris antiqua*, while Good (1979) illustrates similar *Botryopteris* sporangia attached abaxially to small pinnules. Stalks of *Psalixochlaena* sporangia are usually just to one side of a sporangium annulus (Pl. 72, figs. 1, 6; Pl. 73, figs. 3, 4) and are composed of small thin-walled cells that contrast with the somewhat thicker cells of the sporangium wall (Pl. 72, fig. 1; Pl. 73, fig. 4).

EXPLANATION OF PLATE 72

Figs. 1–4, 6–9, *Psalixochlaena cylindrica*. Fig. 5, *Psalixochlaena ramosa*. (A = annulus, F = foliar pinnule, S = sporangium, UP = ultimate pinna). 1. Pair of sporangia sharing a common attachment stalk. 2658A, no. 92, × 125. 2. Cluster of sporangia attached to what is believed to be the abaxial surface of a pinnule. 2658B bot, no. 54, × 37. 3. Pinnule cross-section with marginally attached sporangia. 2658B bot, no. 137, × 40. 4. Ultimate pinna with C-shaped vascular trace and attached sporangium-bearing pinnule. 2658B bot, no. 158, × 40. 5. Ultimate diarch pinna-bearing pinnule with attached sporangium. 231G4 bot, no. 45, × 75. 6. Enlargement of Fig. 4 showing point of sporangium attachment to pinnule (arrow), 2658B bot, no. 158, × 130. 7. Scanning electron micrograph of spore. × 1500. 8. Light micrograph of spore in peel section. Note apparent lack of ornamentation. 2658A, no. 48, × 1250. 9. Stem cross-section typical of the numerous stems found associated with *Psalixochlaena* sporangium-bearing foliar members. 2658A, no. 47, × 40.



GOOD, *Psalixochlaena*

Attachment of sporangia to foliar axes clearly identifiable with *Psalixochlaena* is shown by several specimens. Plate 73, figs. 1, 2 shows a sporangium attached to a wing-shaped piece of tissue believed to be a pinnule cross-section (Pl. 73, fig. 1 at *f*) which is in turn attached to an ultimate pinna. Another sporangium attached to this same ultimate pinna is shown in Plate 73, figs. 2 and 4. Although the vascular trace of this pinna is not preserved, Plate 73, fig. 5 shows that the pinna is organically attached to two higher orders of pinnae, the largest of which (Pl. 73, fig. 5 at arrow) clearly shows a C-shaped xylem trace with protoxylem on the side away from the direction of curvature (Pl. 73, fig. 6). Such a C-shaped trace is characteristic of *Psalixochlaena*, and differs from the tridentate adaxially curved petioles usually produced by *Botryopteris*. A second specimen showing a sporangium attached to a pinnule which is in turn attached to a *Psalixochlaena* ultimate pinna with a C-shaped vascular trace is shown in Plate 72, figs. 4 and 6.

Some sporangia in the *Psalixochlaena* coal ball contain numerous small trilete spores with a triangular outline (Pl. 72, figs. 1–3), measuring from 21 to 29 μm in diameter. When seen in peels (Pl. 72, fig. 8) and in some macerated sporangia the spores appear to lack exine ornamentation. However, spores from many macerated sporangia have a surface covered with numerous short blunt spines (Pl. 72, fig. 7; Pl. 73, fig. 7). Spiny spores correspond to the dispersed spore genus *Acanthotriletes*, while smooth spores would be referred to *Leiotriletes* if found dispersed. In all probability both spore types were produced by plants of the same genus and species. Lack of ornamentation on some spores may be due to developmental or diagnetic factors. In the case of spores found in peel sections, the cellulose acetate of the peel seems to mask the presence of spines which may in fact actually be present (Pl. 72, fig. 8).

DISCUSSION

Based strictly on vegetative features of the plant, *P. cylindrica* was at one time considered part of the genus *Botryopteris*. Recently (Holden 1960; Holmes 1977) the genus had been placed in the Anachoropteridaceae. Now that the reproductive structures of *P. cylindrica* are known, the taxonomic position of this plant should be re-evaluated.

The fertile fronds attributed to *Anachoropteris* sp. by Phillips and Andrews (1965) have sporangia and spores that are unlike those of *Psalixochlaena*. Dennis (1975) suggests that sporangia described by Phillips and Andrews may actually be referable to *Tedelea*, a plant with *Ankyropteris*-like petioles.

Sporangia definitely known attached to *Anachoropteris* fronds include the genera *Sermaya* (Eggert and Delevoryas 1967) and *Doneggia* (Rothwell 1978). Both these genera produce small bluntly triangular smooth-walled spores of a size range similar to the spores of *Psalixochlaena*. Sporangia of *Sermaya* and *Doneggia* are oblong, either stalked (*Doneggia*) or sessile (*Sermaya*), and have a horizontally oblique annulus that extends most of the way around the circumference of the sporangium. This contrasts with the spiny spores and the stalked almost spherical (globose) sporangia of *Psalixochlaena* with a horizontal annulus that extends about half the distance around the sporangium. An important distinction between *Psalixochlaena* sporangia and those known attached to *Anachoropteris* fronds is that *Sermaya* and *Doneggia* sporangia are borne in sori

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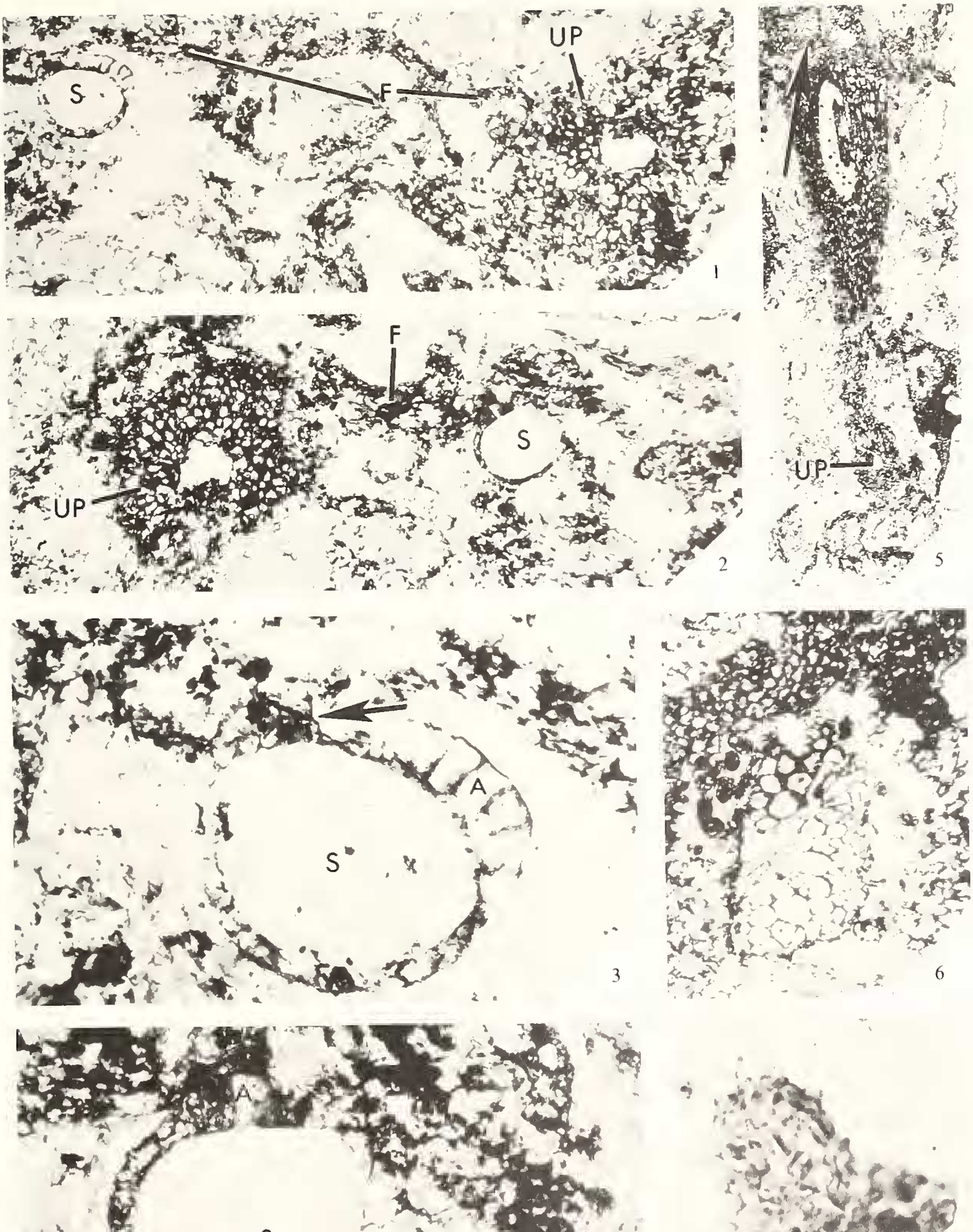
EXPLANATION OF PLATE 73

Figs. 1–7. *Psalixochlaena cylindrica*. (A = annulus, F = foliar pinnule, S = sporangium, UP = ultimate pinna). 1. Cross-section of sporangium-bearing pinnule attached to its ultimate pinna. 2658A, no. 62, ×40. 2. Another sporangium-bearing pinnule attached to the same ultimate pinna shown in Figure 1 of this plate. 2658A, no. 62, ×40. 3. Enlargement of Figure 1 showing point of sporangium attachment to pinnule (arrow). 2658A, no. 62, ×130. 4. Enlargement of Figure 2 showing point of sporangium attachment to pinnule. 2658A, no. 62, ×125. 5. A subsequent peel section of the same ultimate pinna shown in Figures 1 and 2 of this plate illustrating its organic connection to two higher orders of pinnae showing, at arrow, a typical *Psalixochlaena*-like leaf trace (see Fig. 6). This illustration documents the attachment of sporangia shown in Figures 1 and 2 of this plate to axes definitely referable to *Psalixochlaena*. 2658A, no. 71, ×6·3. 6. Enlargement of pinna indicated by arrow in Figure 5 showing the C-shaped *Psalixochlaena*-like vascular trace of this pinna. 2658A, no. 67, ×60. 7. Light micrograph of spiny spore. 2658C maceration, ×1250.



GOOD, *Psalixochlaena*

containing approximately four (*Sermaya*) or many (*Doneggia*) sporangia per sorus. Most *Psalixochlaena* sporangia are borne singly (Pl. 72, figs. 2, 4, 6; Pl. 73, figs. 1–4) or occasionally in groups of two (Pl. 72, figs. 1, 3). Because of their close similarities in sporangial structure and spore type and the fact that both are borne on fronds with *Anachoropteris*-like anatomy, *Sermaya* and *Doneggia* are placed in a single family, the *Sermayaceae*. Although *Psalixochlaena* sporangia are similar to sporangia of the Sermayaceae in spore type and annulus configuration, differences in sporangial shape, and the fact that *Psalixochlaena* sporangia are not borne in sori preclude placing this genus within the Sermayaceae.

Psalixochlaena sporangia and spores described herein appear almost indistinguishable from those of some plants that have to date been placed in the genus *Botryopteris*. Such sporangia are known organically attached to *B. antiqua* of Viséan age (Galtier 1967, 1970) and a *Botryopteris* sp. from the Westphalian A–B boundary (Good 1979) thought to be *B. hirsuta*. Similar sporangia are in association with, and thought to have been borne by, *B. hirsuta* and *B. ramosa* (Seward 1910; Scott 1920). Plate 72, fig. 5 shows what is probably an ultimate pinna of the plant previously known as *B. ramosa* with pinnules bearing an abaxial sporangium similar to a *Psalixochlaena* sporangium. Although not directly attached to this specimen, a stem similar to those described for *B. ramosa* is found a few mm away. No *P. cylindrica* is found in this petrifaction. Diarch pinnae, such as the one illustrated in Plate 72, fig. 5, are known in several species of *Botryopteris* (Holden 1962; Holmes and Galtier 1976). The published literature suggests possible differences between *P. cylindrica* sporangia and those attached to other plants placed to date in *Botryopteris*, but these differences appear minor. For example, no spines are reported on small tetrahedral spores of *B. antiqua*. However, both spiny and spineless spores are seen in the '*Botryopteris* sp.' of Good (1979) and *P. cylindrica*. Lack of spines may be due to preservational or developmental factors, and spines can only be observed in macerated spores. The size range indicated by Good (1979) for the laminar sporangia of North America *Botryopteris* is somewhat smaller than that reported here for *Psalixochlaena*, but a re-examination of the North American specimens has found large sporangia exceeding 400 μm in diameter.

Since the sporangia and spores of *P. cylindrica* and the plants previously called *B. antiqua*, *B. hirsuta*, and *B. ramosa* are so similar, these plants must be very closely related, and this relationship can be used to decide whether or not *Psalixochlaena* should be assigned to the Anachoropteridaceae. Stems of *Anachoropteris* and *Tubicaulis*, the best-known genera of this family, are exarch and have C-shaped petiole traces curving away from the stem, each with three adaxial protoxylem groups. Although *P. cylindrica* has such a petiole trace, and plants currently assigned to *Psalixochlaena* or *Botryopteris* have, typically, three adaxial petiolar protoxylem groups, none of the *Botryopteris* species with *Psalixochlaena*-like sporangia have a C-shaped petiolar trace. Since *P. cylindrica* is obviously closely related to a group of plants that do not have an anachoropterid-like petiole trace, this precludes the assignment of *Psalixochlaena* to the Anachoropteridaceae. Other differences between plants with *Psalixochlaena*-like sporangia and the Anachoropteridaceae include the mesarch stems of *Psalixochlaena* and *Botryopteris*, and the fact that plantlets have rarely been reported in the Anachoropteridaceae. Plantlets (foliar to cauline branching) are apparently common in plants placed to date in the genus *Botryopteris* (Long 1943; Surange 1954; Corsin 1956; Galtier 1970; Phillips 1970) but are as yet unreported in *P. cylindrica*.

The fact that *Psalixochlaena* bears sporangia identical to those produced by some plants currently placed in the genus *Botryopteris* does not necessarily mean that the two genera should be combined. The original description of the *Botryopteris* type species, *B. forensis* (Renault 1875*a*, 1875*b*), includes the fertile parts of the plant, and these fertile structures are quite different from those of *P. cylindrica*. Additional studies (Murdy and Andrews 1950; Galtier 1971; Phillips and Rosso 1970) indicate that all currently known *Botryopteris* species of Westphalian C age or younger in which the reproductive structures are known, have fructifications similar to those of *B. forensis*. These additional plants include *B. globosa*, *B. americana*, and one as yet unnamed species (Phillips 1969). Sporangia of these plants occur in massive aggregations up to 5 cm in diameter, each containing several hundred to several thousand sporangia borne in clusters on or near the ends of ultimate axes which comprise a tightly ramifying fertile axis system. Sporangia are interpreted (Murdy and Andrews 1950) as occupying the positions of pinnules on a fertile frond, as there is no indication of laminar foliage associated with these sporangial aggregations. Individual sporangia are considerably larger (1·0–1·5 mm) and more elongate than *Psalixochlaena* sporangia and have a massive annulus covering the lower portion of the sporangium wall. Spores from these sporangial aggregations are spherical, trilete, have a verrucate exine ornamentation, and correspond to the dispersed spore genus *Punctatisporites*. In sporangium size, shape, annulus configuration, type of spore produced, and particularly in the way sporangia are attached in massive nonlaminar aggregations, the reproductive structures of the *Botryopteris* generitype and other species of the genus that are Westphalian C or younger do not resemble fructifications of *Psalixochlaena* or any pre-Westphalian C plant placed to date in *Botryopteris*.

There is no evidence at all of massive botryopterid sporangial aggregations older than Westphalian C. It was believed that small loose sporangial aggregations borne on fertile axis systems characterized earlier species of the Botryopteridaceae (Galtier 1967, 1970; Phillips 1970). Presently available evidence indicates, however, that at least some pre-Westphalian C botryopterids bore sporangia and spores like those of *P. cylindrica* attached to pinnules and not to fertile axis systems.

Good (1979) described well-preserved *Botryopteris* pinnules from North America bearing abaxial sporangia that are almost indistinguishable from those described in the present report. A similar fertile pinnule, probably of the plant known to date as *B. ramosa* is shown here in Plate 72, fig. 5. Although the question of whether *P. cylindrica* sporangia are borne on axes or on pinnules is not totally resolved due to poor cell preservation of the sporangium-bearing tissues, the evidence is strongly in favour of *Psalixochaena* sporangia being borne on pinnules. The morphology of the sporangium-bearing tissue resembles a pinnule cross-section showing a midvein and an adaxial sporangium. A somewhat similar fertile pinnule is shown in Plate 72, fig. 3. Numerous flat, elongate, poorly preserved bits of tissue resembling pinnules occur in the *Psalixochlaena* coal ball and some have as many as five sporangia attached to what appears to be the abaxial surface (Pl. 72, fig. 2). Attempts to obtain cross-sections of these bits of sporangium-bearing tissue, by recutting the coal ball, have been unsuccessful, suggesting that the tissue does not consist of long narrow axes.

Modern plants are classified primarily on their reproductive structures and not on vegetative features. Applying these criteria to *Psalixochlaena* and *Botryopteris*, it would not be correct to place species bearing sporangia and spores such as those described here in the genus *Botryopteris*. Since Renault's (1875*a*, 1875*b*) original descriptions of the type species, *B. forensis*, clearly recorded the fertile structures of the plant, the large sporangia of the type species with their massive annulus, large *Punctatisporites*-like spores, and aggregation in massive compact groups on fertile axis systems are as important in the concept of the genus *Botryopteris* as the omega-shaped foliar member vascular trace. Even if some pre-Westphalian C plants (e.g. *B. antiqua*) are shown to have *Psalixochlaena*-like sporangia borne loosely on fertile axis systems instead of on pinnules, as suggested by Galtier (1967, 1970), differences between sporangia of the older botryopterids and sporangial aggregations of the type species *B. forensis* and other members of the genus *Botryopteris* Westphalian C and younger would be enough to warrant excluding from *Botryopteris* all plants with *Psalixochlaena*-like sporangia. These differences include sporangium size, shape, annulus position, and type of spore produced. It is therefore proposed that the concept of the genus *Psalixochlaena* should be altered to include all plants with sporangia and spores such as those described here. All pre-Westphalian C plants previously called *Botryopteris* which are thought to bear such sporangia and spores are transferred to *Psalixochlaena*. Such sporangia are known to have been produced by the plant previously called *B. antiqua* both by association and by probable attachment (Galtier 1967, 1970). Both Seward (1910) and Scott (1920) note the presence of small sporangia-bearing tethedral spores, triangular in outline, associated with species previously named *B. ramosa* and *B. hirsuta*. Good (1979) suggests that laminar sporangia may be referable to *B. hirsuta*. The specimen illustrated here in Plate 72, fig. 5 is probably referable to what has been called *B. ramosa*, the most common botryopterid at the Burnley locality. *Psalixochlaena birwickense* Long (1976) will be left in the genus even though the species is known only from vegetative specimens.

Psalixochlaena is the most appropriate genus to use because it is the only validly published genus, other than *Botryopteris*, in which reproductive structures such as those described here are known by attachment. When *Psalixochlaena* was first erected by Holden (1960) the genus was based strictly on anatomical features and as such may have been an invalid genus, since there appear to be no fundamental differences anatomically between *Psalixochlaena* and the previously existing Upper Pennsylvanian age genus *Apotopteris* (Morgan and Delevoryas 1954). In both genera there are several mesarch protoxylem groups in the stem. The abaxially curved petiole traces of both genera appear very similar to each other. The peripheral small tracheids in the stem of *A. minuta*, which Morgan and Delevoryas suggest might represent part of the protoxylem, are clearly seen in cross-sections of *P. cylindrica* stems (e.g. Holmes 1977, Pls. 3 and 4). Although it is possible that *P. cylindrica* should originally have been designed as a species of *Apotopteris*, the reproductive organs of *Apotopteris* are currently unknown, and thus it is not appropriate at this time to use *Apotopteris* to link together plants with sporangia like those described in this report. There is a possibility that *Apotopteris* or some plants with *Botryopteris*-like petioles from the Upper Pennsylvanian bore sporangia and spores similar to those of *Psalixochlaena*. Mamay (1950) described such sporangia from the *Apotopteris*-type locality and similar Upper Pennsylvanian age sporangia are under investigation by the present author.

Fertile structures of *Psalixochlaena* suggest that this genus should be assigned to the family Botryopteridaceae. The phyletic lines suggested by Phillips (1970) and Galtier and Phillips (1977) between species now placed in *Psalixochlaena* and true species of *Botryopteris*, as well as the existence of a fructification that appears intermediate between *Psalixochlaena* and *Botryopteris* (Millay and Taylor 1978) provide good justification for assigning *Psalixochlaena* to the Botryopteridaceae.

The genus *Psalixochlaena* as delimited in the present report extends from the Viséan through the Westphalian B. Current research in my laboratory may extend the range of this genus through the Stephanian (Upper Pennsylvanian) to include some plants of this age currently placed in the genera *Apotopteris* and *Botryopteris*. There is at least a possibility that plants with *Psalixochlaena*-like sporangia may have continued beyond the Carboniferous and include ancestors of the modern fern family Osmundaceae (Galtier 1967; Good 1979).

SYSTEMATIC PALAEOBOTANY

Family BOTRYOPTERIDACEAE Renault 1896.
Genus *PSALIXOCHLAENA* Holden 1960.

Emended diagnosis. A fern possessing a slender stem with immature parts densely clothed with unbranched multicellular hairs. Stem protostele with mesarch protoxylem. Petioles arising from stem in 2/5 phyllotaxy, circinately coiled when young. Petiole and major pinnae (foliar members) xylem trace with three protoxylem ridges on adaxial surface, more if about to branch. Ultimate pinnae with two or three protoxylem ridges. Roots adventitous. Sporangia small (250–425 μm diam.), globose except for bulge on side caused by the annulus, a lateral band 1–2 cells thick and extending approximately half-way around the sporangium. Sporangia stalked, occurring singly or in groups of two, attached abaxially or sometimes marginally to fertile pinnules or attached to fertile axes. Large aggregations of sporangia not present. Spores small (25–40 μm diam.), trilete, triangular as seen in polar view, and when well preserved usually covered with short blunt spines.

Type species. *Psalixochlaena cylindrica* Holden 1960; emend Holmes 1977.
Additional species. *P. antiqua* (Kidston 1908; emend Holden 1962; emend Phillips 1970) comb. nov.
P. hirsuta (Scott 1899; emend Phillips 1970) comb. nov.
P. ramosa (Scott 1900; emend Phillips 1970) comb. nov.
P. birwickense Long 1976

Acknowledgements. This study was supported by the National Science Foundation (DEB76-21410) and the Lima Campus Research Committee.

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Typescript received 30 January 1980
Revised typescript received 12 May 1980